

Heterospory and seed habit of Pteridophytes

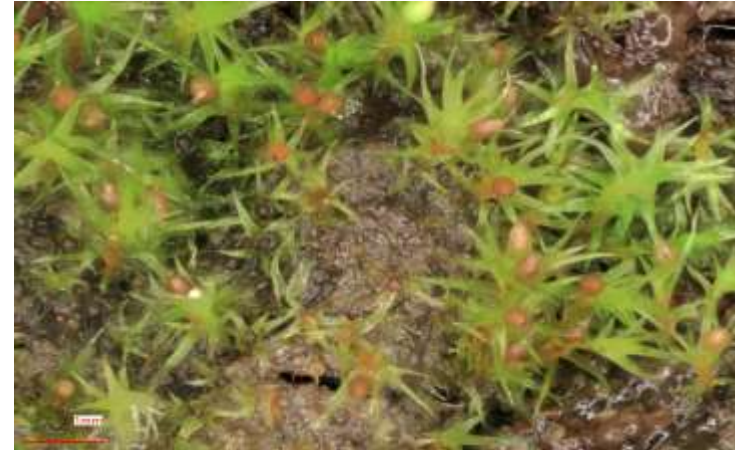
Introduction

Early land plants- Bryophytes were predominantly homosporous except *Micromitrium*

Homosporous meaning- plant producing only one type of spore that is uniform in size and shape

Micromitrium produces smaller and larger spores in the same sporangium

Sporangium meaning –specialized structure or capsule on the sporophyte plant that produces and contains spores



<https://www.britishbryologicalsociety.org.uk/learning/species-finder/micromitrium-tenerum/>

These two different spores remains to be determined whether they germinate to produce gametophyte of two sexes (♂ ♀)

Heterospory:

- Production of two kinds of spores differing in structure and function
- Smaller one producing- male gametophyte
- Larger one producing- female gametophyte
- Heterospory is an interesting concept because of its bearing on the evolution of seeds
- It brings in a new type of gametophyte
- Endosporic- which is a biological advancement over exosporous gametophyte of homosporous forms

Exosporic gametophyte meaning- type of development where the haploid gametophyte stage grows outside of the original spore wall upon germination

Female gametophyte (which are Developing within large megaspore, endosporous type)

- At the expense of reserve food
- Independent of external environment
- Better place for the initiation of embryo

Female gametophyte (which are free living exosporous type)

- Green prothalli of homosporous forms
- Dependent on external environment
- Have to be self supportive in food supply

1st distinct heterospory, structural as well as functional was evident in pteridophytes

Only 9 genera among the several group of pteridophytes, (*Selaginella*, *Isoetes*, *Stylites*, *Marsilea*, *Pilularia*, *Regnellidium*, *Salvinia*, *Azolla* and *Platyzoma*) are heterosporous and some are considered to approach the seed habit



Selaginella



Isoetes



Marsilea



Pilularia



Regnellidium



Salvinia



Azolla



Platyzoma

Incipient heterosporous forms

An account of Heterospory should begin with forms showing incipient heterospory

Equisetum

- Homosporous
- But produce two types of gametophytes
- Smaller ones- male; Larger ones- Female
- The later becomes hermaphrodite if fertilization is delayed

In population, proportion of male and female gametophyte is influenced by environmental conditions

Sex determination, occurs during vegetative phase of gametophyte



Ceratopteris thalictroides

- Monotopic fern, homosporous fern
- Produce male and female gametophytes
- Proportion is not influenced by environmental conditions
- Female gametophyte- produce antheridia if fertilization is delayed



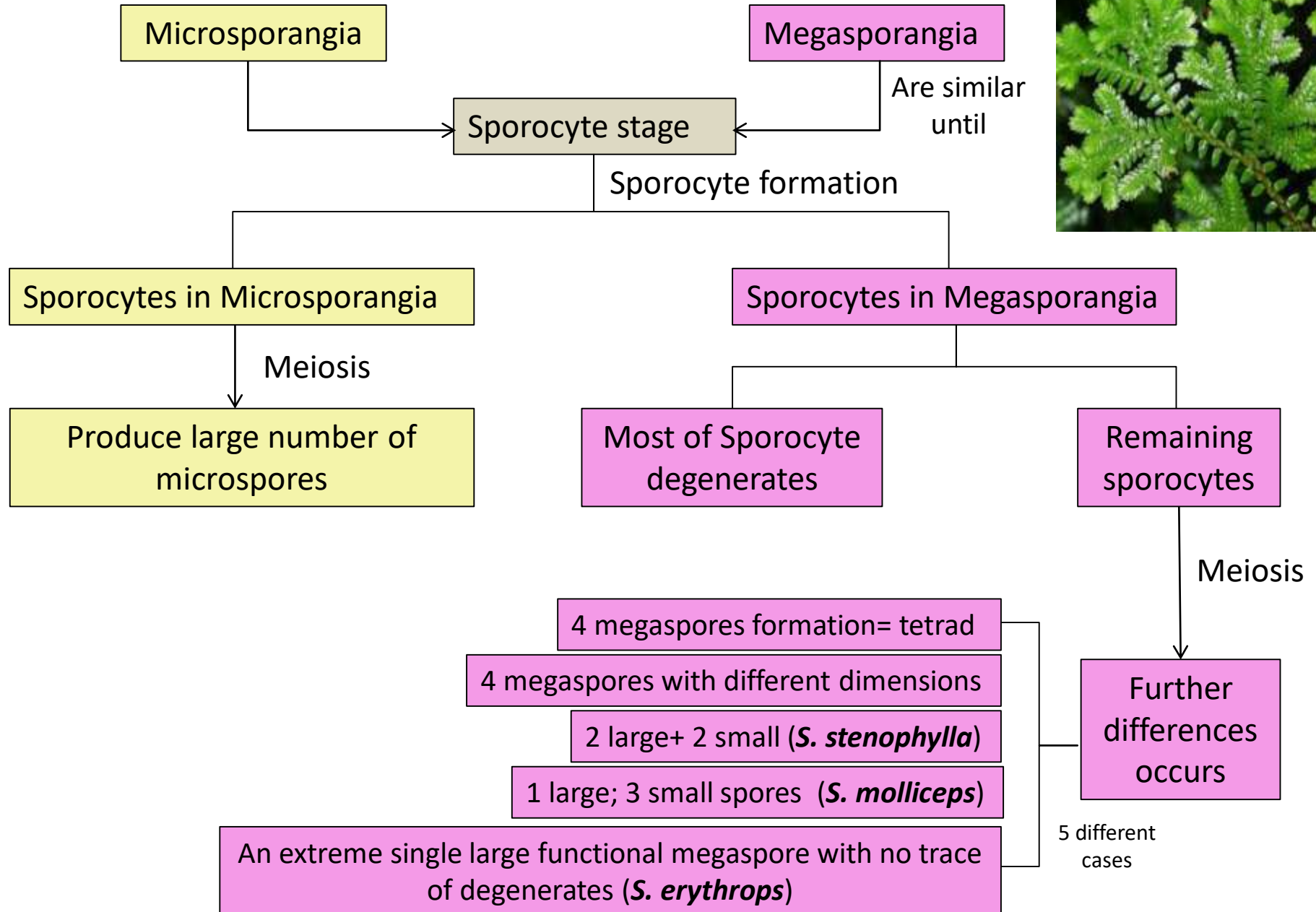
Platyzoma

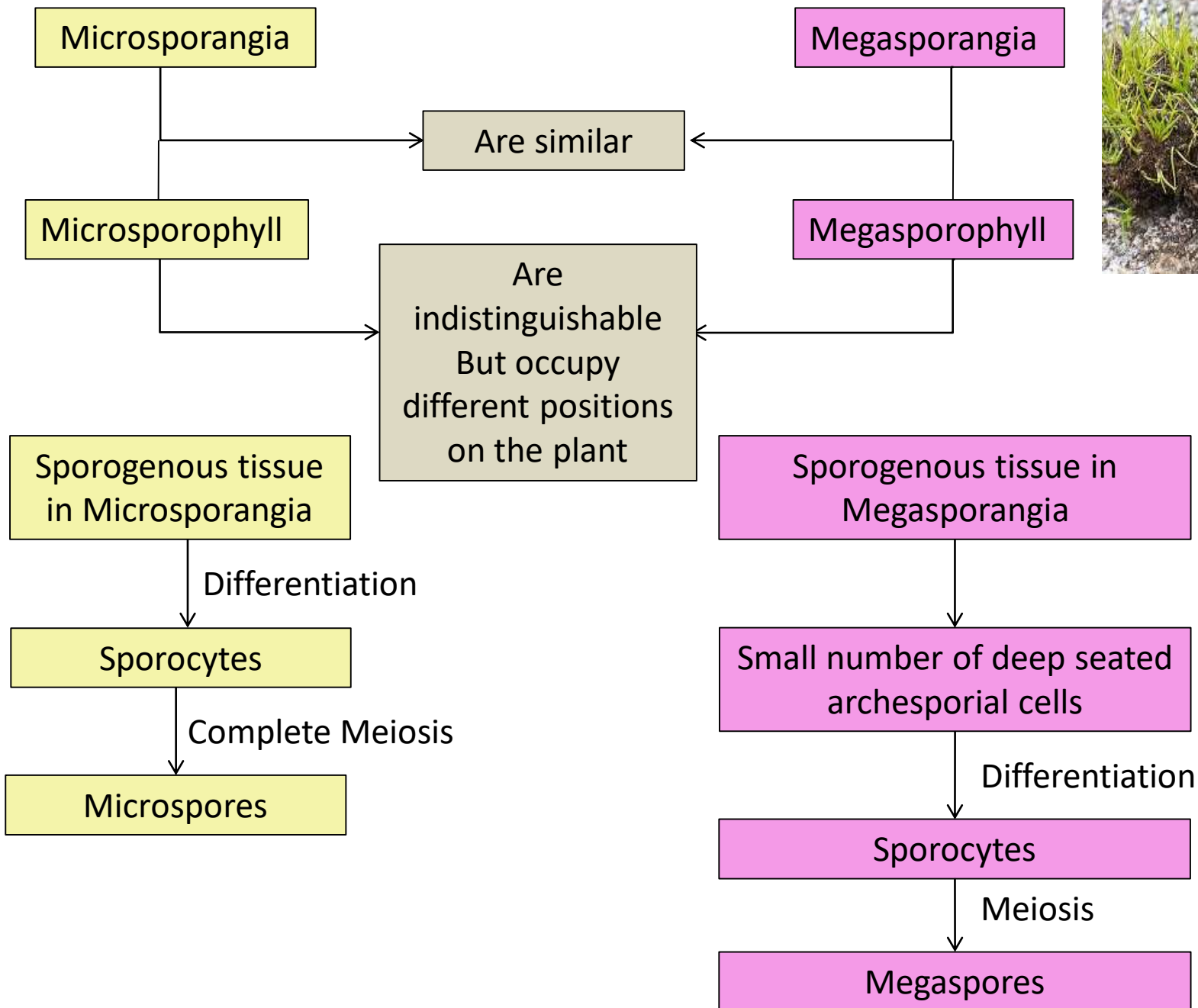
- Queensland fern
- Intermediate between forms showing incipient heterospory and complete heterospory (heterothallism)
- Sporangia- similar in size and occur intermingled but spore size and number of spores in each sporangium is different
- 16 megaspores- germinate to produce filamentous male gametophytes
- Megaspores- form archegoniate gametophytes that develop into antheridia if fertilization is delayed
- It is heterosporous form with a latent homosporous
- Therefore evidences indicate that heterothallism might have preceded heterospory in evolution

**Developmental events
and heterospory**

The perusal of the forms showing heterospory indicates that most significant events in the determining process are:

1. Time of sex determination
2. Number of archesporial cells in sporangia
(Whether archesporial cells directly differentiate as sporocytes or divide mitotically thereby increasing the number of sporocytes)
3. Number of sporocytes initiating and completing meiosis
4. Number of spores attaining maturity

In *Selaginella*

In *Isoetes*

Microsporangia

Megasporangia

Differences do not appear until meiosis

Sporogenous tissue in
Microsporangia

Differentiation

Sporocytes in Microsporangia

↓
Meiosis

Produce 64 microspores

All Matures

Sporogenous tissue in
Megasporangia

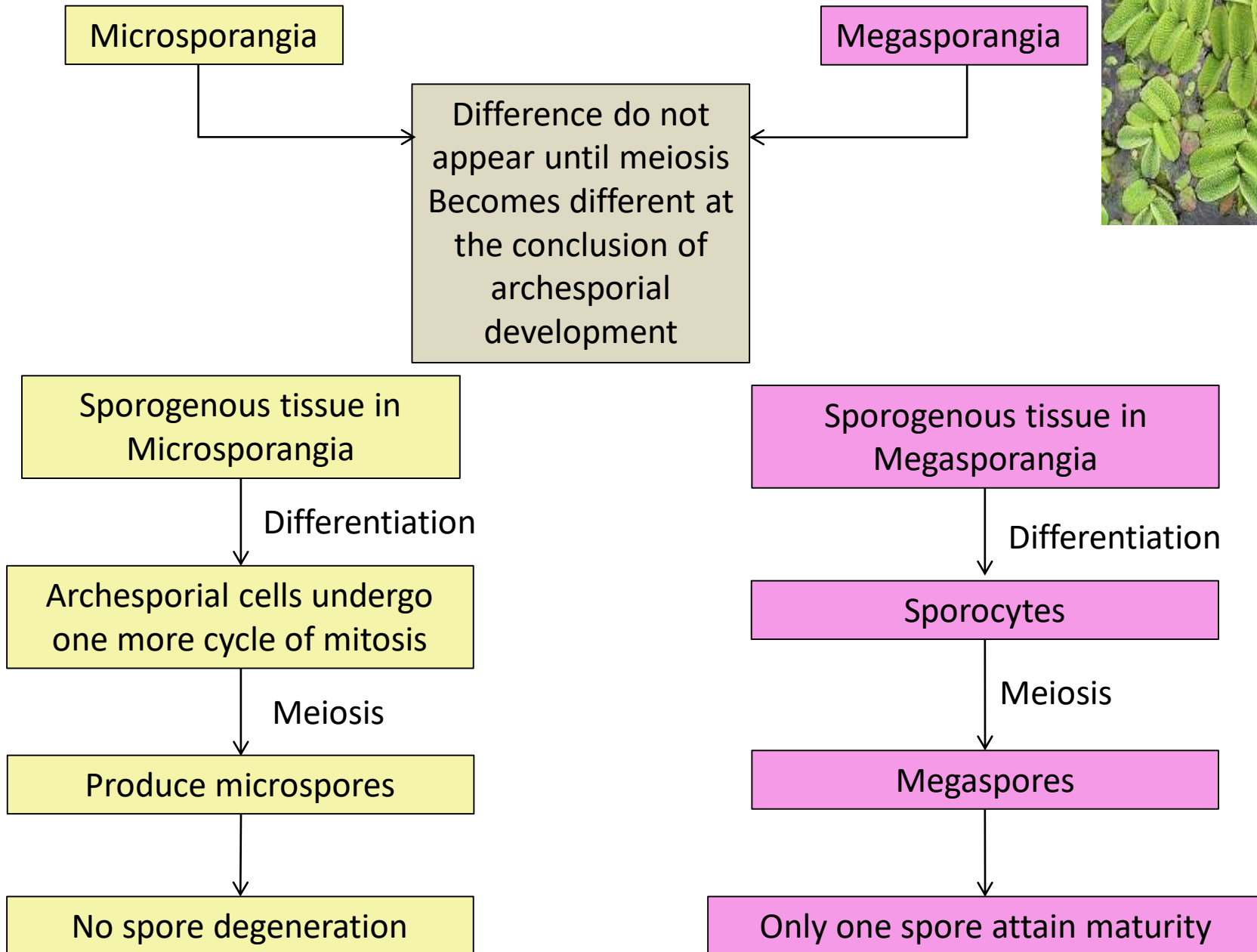
Differentiation

Sporocytes in Megasporangia

↓
Meiosis

Produce 64 megaspores

Only one is able to attain maturity

In *Salvinia*ceae

Inference:

- The determining processes leading to heterospory are operative at different stages of development and no generalization can be made
 - In lower pteridophytes (***Selaginella***) determining process is operative at premitotic as well as post mitotic stages
 - In ***Isoetes*** operative only at premitotic stage
 - In higher pteridophytes (***Marsilea***) the control is postmeiotic
 - In ***Salviniaaceae***, Premeiotic as well as post meiotic

In *Selaginella pilifera*

Microsporangia

Megasporangia

Different

Microsporangial
primordium

Slightly smaller than

Megasporangial
primordium

The entire sporogenous
tissue in a
microsporangium shows
uniform staining

During development,
All sporocytes except
one show loss of RNA
stainability

All microsporocytes prior to
meiosis are surrounded by
distinct callose walls

Only the functional
megasporeocyte shows
callose walls

The presence or absence of callose wall around developing sporocyte- is suggested to isolate it from surrounding cells and facilitate it in its new developmental pathway

Fossil record and heterospory :

Indicates heterospory is of quite early occurrence and was widespread in pteridophytes of the past

Many had attained advanced level of heterospory approaching the seed habit and some suggest possible origin of heterospory

Paleontological record shows, the earliest vascular plants were homosporous and probably produced Exosporic Monoecious gametophytes similar to present day homosporous forms

In lowermost strata of upper Devonian (Frasnian stage) a free sporing heterosporous condition was attained

Free sporing heterosporous condition/ stage meaning in which spores are heterosporous but produce exosporous gametophyte Ex. ***Barinophyton***

From free sporing homospory evolved the free-sporing heterospory

Initial steps of heterospory, are revealed by ***Calamostachys*** a fossil sphenopsid and archiac form of present day ***Equisetum***

The genus has homosporous as well as heterosporous forms and the size of surviving spores is related to number of degenerating spores

Reduction in number of megaspores revealed by ***Archaeopteris***

Macrophyllous, with gymnospermous anatomical characters and pteridophytic reproductive structures

In upper Devonian period, the number of spores in ***Archaeopteris***, megasporangium was being reduced

Extensive spore degeneration in megasporangium shown by ***Stauropteris burntislandica***

The megasporangium of ***Stauropteris burntislandica*** features,

- Basal half or more of the sporangium is sterile possibly serving as food reservoir
- Slender vascular strand running through the sterile portion. This is the most extensive vascularization of any fern/ fern like sporangium
- Few specimens show a tapering apex with a minute opening

It is a specialized megasporangium but not seed

Environmental factors and Heterospory :

- Nutritional and environmental factors possibly influence the pattern of development
- Shattuck (1910) found that spore development can be manipulated by environmental factors
- Under favorable nutritive conditions:
 - Spores in developing Microsporangia aborted and the survivors enlarged
 - The enlargement was proportional to degeneration and spores enlarged upto 16 times their normal size
 - Rarely single spore survived and in its cytological features; such as vacuolation, nuclear shape and position to the cell it resembled the megaspore
- Plants grown in unfavorable nutritive conditions:
 - Microspores found in sporangia, by their position at the tip of sorus, would contain megaspores
- However these altered spores were not made to germinate and it is therefore, not certain whether alteration were mere structural or functional

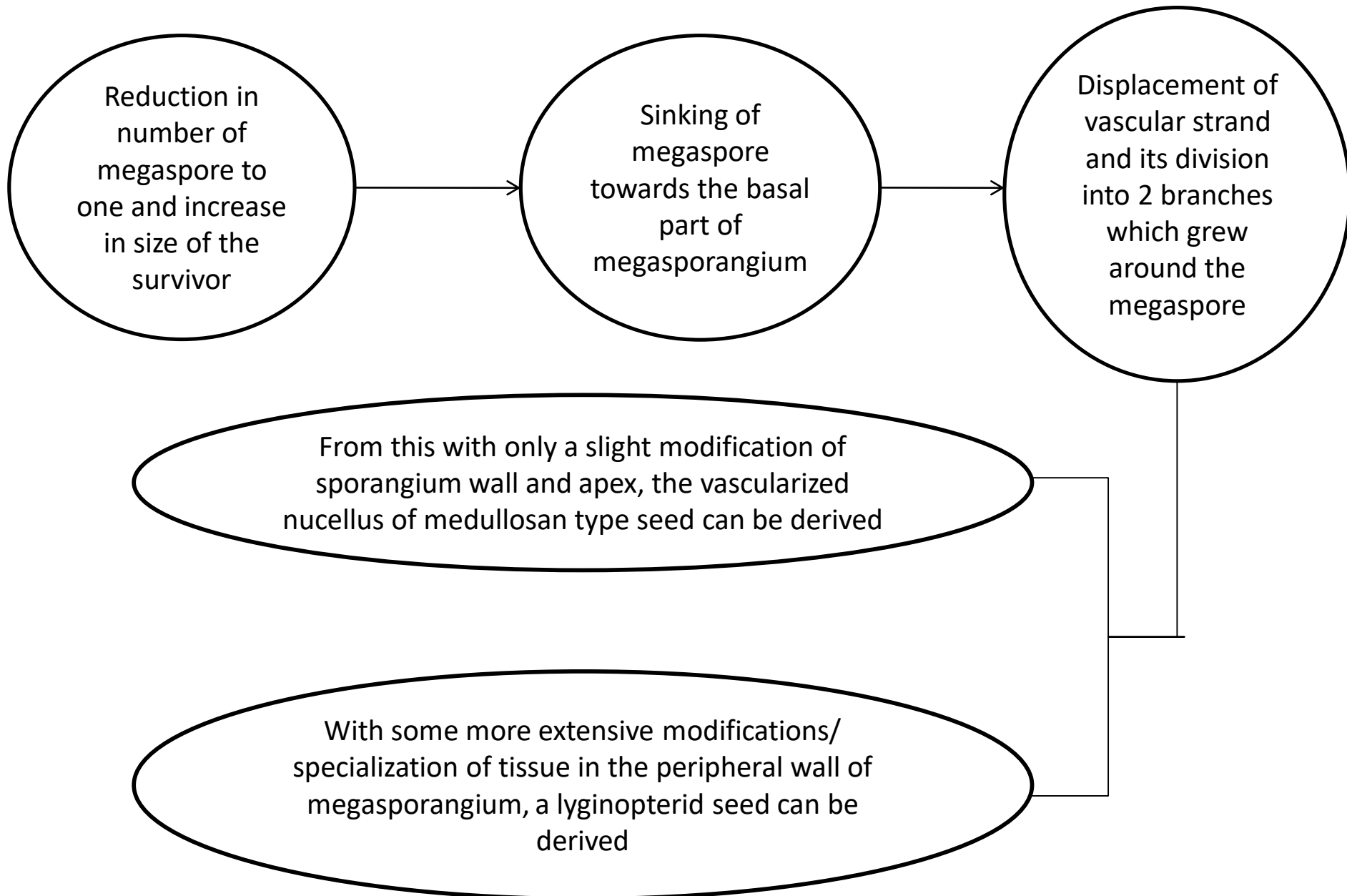
Origin of seed

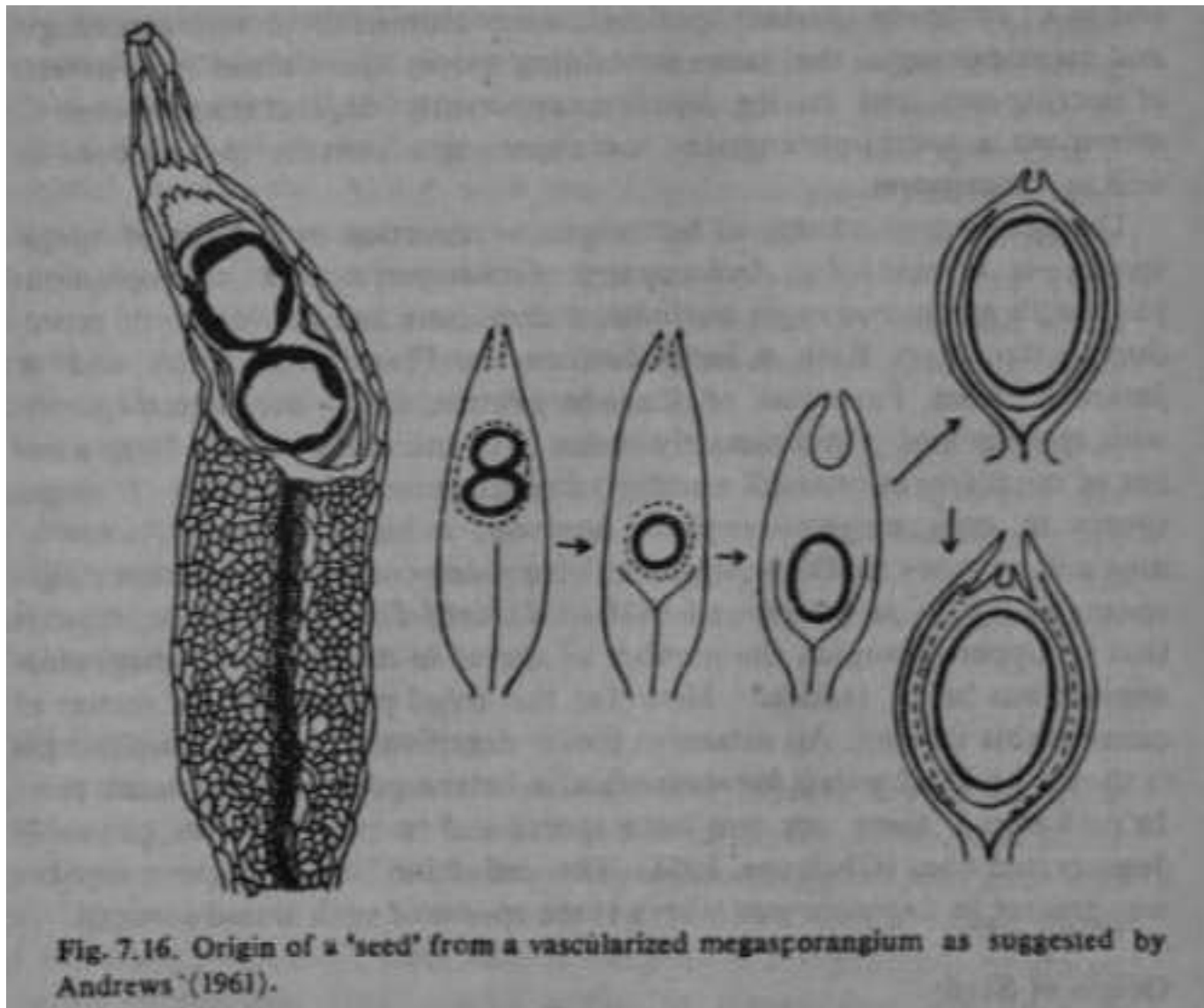
An evolutionary sequence of origin of seed from homosporous form should involve,

- Production of two kinds of spores
- Reduction in the number of functional megaspores to a single megaspore in the sporangium
- Retention of megaspore within the megasporangium
- Elaboration of megasporangium apex for microspores reception
- Formation of integuments- a new structure with micropyle

According to Andrews (1966),

A seed can be conceived to have evolved from it involving 3 steps:





<https://archive.org/details/introductiontopt0000rash/page/186/mode/2up>

To summarize,

1. **Pteridophytes** (ferns and allies) are spore bearing vascular plants lacking seeds
2. However some pteridophytes exhibit traits that likely led to the evolution of the seed habit in gymnosperms and angiosperms

3. The reproductive pattern of pteridophytes include:

Homosporous type

Most ferns produce single type of spore – bisexual gametophyte (produces both male and female gametes in one)

Heterosporous type

Some pteridophytes (***Selaginella*, *Isoetes***) produce two types of spores:
 Microspores- male gametophyte (produces male gametes)
 Megaspores- female gametophyte (produces female gametes)

Significance- heterospory is a key step towards seed evolution

Selaginella (a pteridophyte) is an example of an intermediate form which shows characteristic features:

- Heterosporous
- Ligulate leaves
- But still no seeds

Shows a transition towards seed plants (retains megaspore, but lacks integuments and true seeds)

Steps led to seed habit:

1. **Heterospory**- separate male and female gametophyte- reduce self fertilization, promotes genetic diversity
2. **Retention of megaspores**- the megaspore is retained within the megasporangium (nucellus); the female gametophyte develops inside the sporangium, nourished by the parent plant (*Selaginella*) but more advanced in gymnosperms
3. **Development of integuments**- In pteridophytes, sporangia are naked, in seed plants, the megasporangium is enclosed by integuments- forms the ovule (protection and nourishment)
4. **Pollination and siphonogamy**- Pteridophytes- sperm swim to egg (water dependent); in Seed plants- tube delivers sperm (independent of water)
5. **Fertilization and seed formation**-
 1. Seed habit
 2. Fertilization → Zygote → Embryo(retained within the seed) (ovule- seed)
6. **Seed = Protected embryo + Stored food + Protective coat** (absent in pteridophytes)